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Electronoyesella antiqua Simutnik, gen. et sp. nov. (Chalcidoidea, Encyrtidae) from Rovno amber

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Abstract

Electronoyesella antiqua Simutnik, **gen. et sp. nov.**, is described and illustrated based on a female specimen from late Eocene Rovno amber. Like most previously described Eocene Encyrtidae, the new taxon differs from the majority of extant ones in a number of features. Sclerotised metasomal structures, similar to the paratergites of extant Tetracneminae, are seen here for the first time in fossils. The new genus is characterized also by the frontovertex with four vertical rows of piliferous punctures and the face also with intricate sculpture; notauli are present as small but distinct depressions, only anteriorly; the apex of metatibia with a peg originating from a round, deep pit; and the unusual setation of the hind wing.

Keywords

cerci, Eocene, evolution of Encyrtidae, metatibial peg, paratergites

Introduction

To date, 16 species in 14 extinct genera of Encyrtidae have been described from Rovno, Baltic, and Danish ambers and several undescribed encyrtids have been reported by Noyes and Hayat (1994) and Manukyan (1999) from Baltic amber. Extinct Encyrtidae demonstrate remarkable morphological differences from extant representatives of the

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family (Simutnik et al. 2014, 2021a, b, 2022a, b; Simutnik 2015a, 2021; Simutnik and Perkovsky 2018). Most examined European amber Encyrtidae differ from the majority of extant ones by their relatively long marginal vein in the forewing, a distinctly thickened but not triangular parastigma, a short radicle, and a seta marking the apex of the postmarginal vein not longer than any other on this vein. Many have cerci positioned apically or subapically (Simutnik 2021).

One species of the extant genus *Copidosoma* Ratzeburg, 1844, *C. archeodominica* Zuparko & Trjapitzin, 2014, has been described from Miocene Dominican amber (Zuparko and Trjapitzin 2014).

According to the molecular analysis of Peters et al. (2018), Encyrtidae had already split into two subfamilies in the middle Eocene. Encyrtidae with filum spinosum (the presence of which is one of the main features of Encyrtinae; Trjapitzin 1968) are known since late Eocene (Simutnik et al. 2014, 2020), not from middle Eocene Sakhalinian amber (Simutnik 2015b, 2021). Further, although paratergites (their presence between the syntergum and the outer plates of the ovipositor is one of the main features of Tetracneminae; Trjapitzin 1968) have not been previously found in fossil encyrtids, at least similar structures are reported here for the first time.

Materials and methods

The studied specimen is housed in the collection of the Schmalhausen Institute of Zoology of the National Academy of Sciences of Ukraine, Kiev (SIZK). The amber piece containing the holotype (0.95 grams after primary preparation) was found in the Pugach quarry (Klesov) (fauna of the deposit reviewed by Mitov et al. 2021), Sarny District, Rovno Region.

The specimen was examined using the equipment and techniques described in Simutnik et al. (2022a). Photographs were taken using a Leica Z16 APO stereomicroscope equipped with a Leica DFC 450 camera and processed with LAS Core and Adobe Photoshop software (brightness and contrast only).

Terminology and abbreviations follow Sharkov (1985), Gibson (1997), and Heraty et al. (2013). For the identification, comparison, and description of the new taxon, we also used the keys of V.A. Trjapitzin (1989); J.S. Noyes, J.B. Woolley, and G. Zolnerowich (in Gibson 1997); and the genus description of *Oesol* Noyes & Woolley, 1994 (Noyes, Woolley 1994). We use the following abbreviations: **FS** = filum spinosum; **F1, F2, etc.** = funicular segments 1, 2, etc.; **LOL** = minimum distance between the anterior ocellus and a posterior ocellus; **mps** = multiporous plate sensilla; **OOL** = minimum distance between an eye margin and the adjacent posterior ocellus; **OCL** = minimum distance between a posterior ocellus and the occipital margin; **POL** = minimum distance between the posterior ocelli; **OPO** = outer plates of the ovipositor. Other abbreviations are explained in figure captions.

Results

Systematic paleontology

Chalcidoidea Latreille, 1817
Encyrtidae Walker, 1837
Tetracneminae Howard, 1892

Genus *Electronoyesella* Simutnik, gen. nov.
https://zoobank.org/5BFACFC4-6923-4E7B-B034-95DEEE352D78

Type species. *Electronoyesella antiqua* Simutnik, sp. nov.

Species composition. Type species only.

Etymology. The new genus is named in honor of John Stuart Noyes, who first saw the presence of the structures similar to paratergites in the new fossil. The name is a combination of "electrum" (Latin: *electrum* = amber) and "Noyes". The genus name is a feminine noun.

Diagnosis. Female. Body not flattened; frontovertex as long as broad, with four vertical rows of piliferous punctures (Fig. 3A); ocelli forming right angled triangle; horizontal row of three large, deep cells under each torulus (Fig. 4); clypeus and interantennal prominence intricately sculptured; mandibles tridentate with middle tooth longest; scape much more than 3× as long as broad; F1 a little longer than broad to quadrate; notauli present only anteriorly as small but distinct depressions (Fig. 3B: arrow), without visible lines; filum spinosum absent; covering setae present; marginal vein 5× as long as broad; postmarginal vein 1.5× as long as marginal; costal cell of hind wing with line of long setae (Fig. 5C: ls1), longest of which located alongside parastigma (Fig. 5C: pst); row of thickened setae present alongside hyaline spur vein of hind wing (Fig. 5C: ls2, spv); apex of metatibia with one peg (Fig. 2A: arrows); cerci located in apical third of metasoma; paratergite-like, sclerotized, separated part of Mt8 present alongside margin of syntergum (Figs 6A, B, 7C: ptrg?); apex of hypopygium reaching a little way past apex of last gastral tergum.

Male. Unknown.

Remarks. Placement of *Electronoyesella* gen. nov. in Tetracneminae is supported by the absence of the filum spinosum of linea calva, the tridentate mandibles with the middle tooth being the longest, the hypopygium reaching a little way past the apex of the syntergum, and the presence of the sclerotized, ribbon-like, separated part of Mt8 along the margin of the syntergum (Figs 6A, B, 7C: ptrg?). This structure closely resembles the paratergites of extant Tetracneminae (Fig. 7A, B: ptrg) and may be morphological evidence for the existence of this subfamily in the late Eocene.

The hind wing of the new genus has a single line of long setae alongside the entire costal cell (Fig. 5C: ls1) as in most extant Tanaostigmatidae. These setae vary in length, the longest located along the parastigma of the hind wing. In fossil Encyrtidae, the

same line of long setae has been recorded in *Eocencnemus sugonjaevi* Simutnik, 2002, *Sulia glaesaria* Simutnik, 2015 (Simutnik et al. 2021), and is also known in several undescribed specimens without filum spinosum. These differ from the new genus by the absence of a vertical rows of large piliferous punctures on the frontovertex. *E. sugonjaevi* also differs by its short, ring-like F1.

The same line of long setae alongside the costal cell of the hind wing is present in few extant Encyrtinae: *Exoristobia* Ashmead, 1904 (Simutnik et al. 2021), *Rhytidothorax* Ashmead, 1900, and some other Bothriothoracini Howard, 1895 (J. S. Noyes, pers. comm. 2022). In *Aphycoides* Mercet, 1921 these setae are sparser and shorter. Within Tetracneminae, a somewhat similar line of setae is present in *Ericydnus* Walker, 1837 and *Moraviella* Hoffer, 1954, but their setae do not vary in length. A line or several lines of setae are present in *Aenasius* Walker, 1846; *Blepyrus* Howard, 1898; *Monodiscodes* Hoffer, 1953, but they are also short.

A line of long setae, but sparser and more or less equal in length originating from the membrane of the costal cell, similar to these of *Ericydnus*, are also found in the earliest known Sakhalinian amber encyrtids: *Sugonjaevia* Simutnik, 2015, *Encyrtoides* Simutnik, 2021, and *Sakhalinencyrtus* Simutnik, 2021. This character state seems to be a feature of the stem group of Encyrtidae.

The first funicular segment seen in the majority of known Eocene encyrtid females, including the oldest described female from middle Eocene Sakhalinian amber (Simutnik 2021), had an annular shape, or at least is broader than long. Of the 27 examined females of European and Sakhalinian ambers (some of which might belong to the same species), some undescribed, few have an F1 longer than broad. Among Eocene females without the filum spinosum (supposedly Tetracneminae), only in *Sulia* Simutnik, 2015 and *Rovnopositor* Simutnik, 2022, is F1 about 1.5× as long as broad (the latter differs from the new genus by the absence of vertical rows of piliferous punctures on the frontovertex, its shorter marginal vein, the reduced gonostyli, and by its long, curved ovipositor stylet). F1 in *Electronoyesella* is slightly longer than broad (Fig. 3A, B).

The new taxon further differs from most known Encyrtidae by the presence of a peg or spicule originating from the round, deep pit at the apex of metatibia (Fig. 2A, arrows); and a row of thickened setae alongside the spur vein of the hind wing (Figs 5C, 6B: spv). Such a row of setae is also absent in the middle Eocene encyrtids from the Sakhalinian amber.

Electronoyesella antiqua **Simutnik, sp. nov.**
https://zoobank.org/E78EBF78-2533-4025-98F2-B486BA6E3736
Figs 1–6, 7C

Material. ***Holotype***, SIZK K-27005, 1 ♀, Klesov, Sarny District, Rovno Region, Ukraine; Rovno amber; late Eocene (deposited in SIZK). The inclusion is in a reddish-yellow and clear, parallelepiped piece of amber (ca. 7 × 6.5 × 4 mm). It is well preserved, but its left side is obscured by a large air bubble (Figs 1B, 2).

Figure 1. *Electronoyesella antiqua* gen. et sp. nov., holotype female **A** body, lateral view **B** body, antero-dorsolateral view.

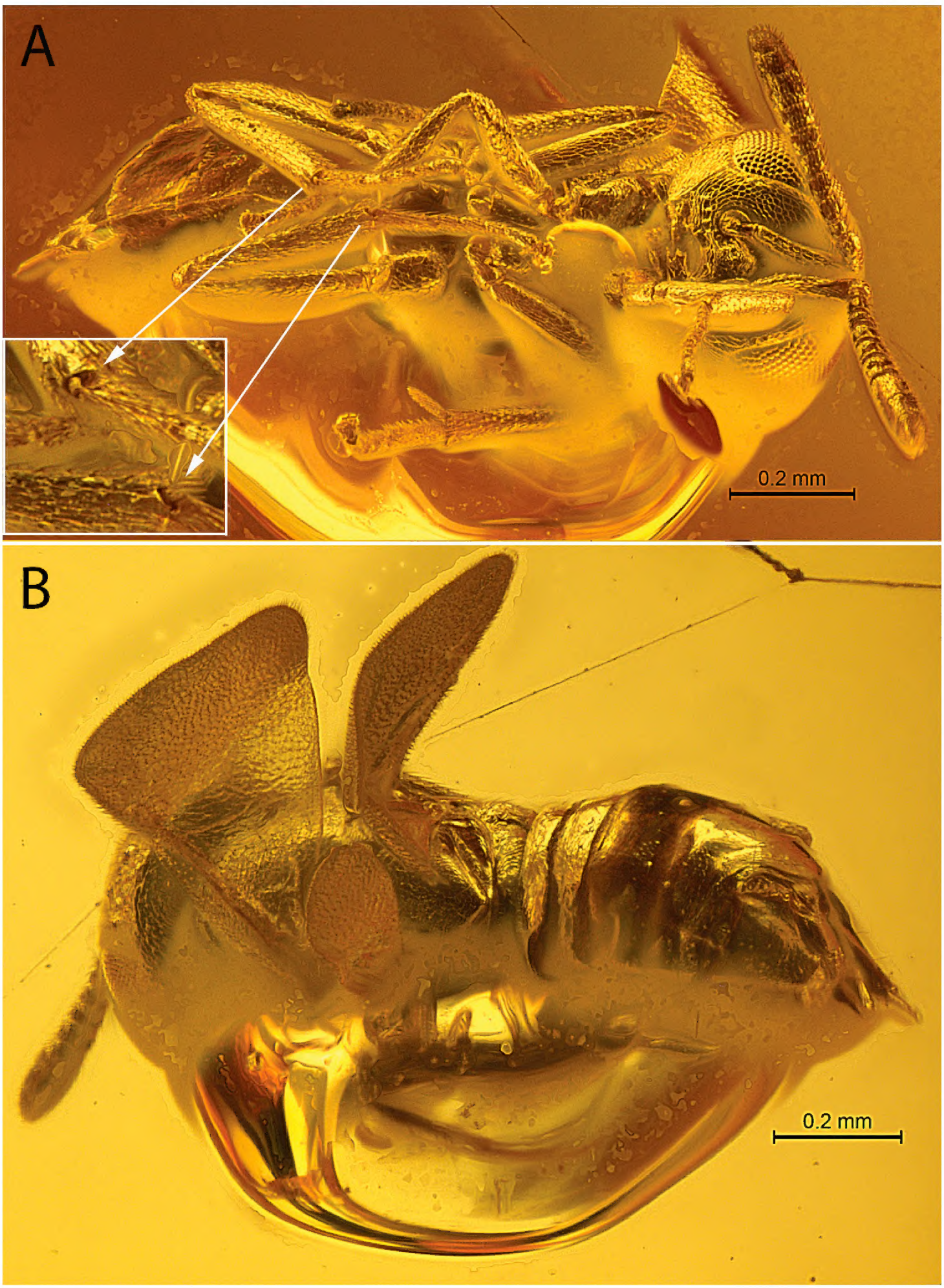

Figure 2. *Electronoyesella antiqua* gen. et sp. nov., holotype female **A** body, ventral (arrows indicate the metatibial pegs in inset) **B** body, posterodorsal.

Syninclusions. Nematocera, spider web.
Etymology. The specific epithet means ancient in Latin.
Description. Female. Habitus as in Figs 1, 2. Body length 1.3 mm.

Coloration. Head, thorax, gaster dorsally, tegula, and all femora black; antenna uniformly dark brown; gaster ventrally dark brown; venation brown; mesotibial spur and tarsi pale yellow; surface of frontovertex, thorax, legs shiny due to presence of a thin layer of air, without metallic shine.

Sculpture. Head, pronotum and mesoscutum rough reticulate, but surface of head only sparsely punctate – frontovertex with 4 vertical rows of large but shallow piliferous punctures (Fig. 3A), outer row separated from eye margin by a distance equal to or more than diameter of this punctures; scape, pedicel, scutellum, tegula, mesopleuron, coxae, legs, and gaster also relatively similarly but more smoothly reticulate; sculpture of face as in Fig. 4 – horizontal row of three large, deep cells located under each torulus, lateral to clypeus, also intricately sculptured.

Head. Lenticular, slightly wider than thorax in dorsal view; occipital margin sharp, but not carinate (Fig 2B); frontovertex curved to posterior ocelli; broadly rounded in frontal view, not vaulted above eyes; eyes bare, without visible setae, with inner orbits parallel over much of height but ventrally divergent (Figs 3B, 4); frontovertex as long as broad, minimum distance between eyes about 0.4× head width; ocelli forming a right angled triangle, posterior ones closer to eye than occipital margin; OOL about equal to posterior ocellar diameter; OOL:POL:LOL:OCL about 3:11:8:4; eye reaching occipital margin (Figs 1A, 3); antennal scrobes as in Figs 3, 4, v- or u-shaped and meeting dorsally, not extended to anterior ocellus, in dorsal view anterior ocellus about equidistant from occipital margin and from upper margin of scrobal depression; interantennal prominence presents (Fig. 4); antennal toruli located about at level of lower eye margin, separated from mouth margin by distance equal to their own width (Fig. 4); distance between toruli equal to distance between torulus and eye, about 1.5× width of torulus, about 0.5× length of malar space; malar space with complete malar sulcus (Fig. 4), about 2× shorter than height of eye; clypeus strongly emarginate, with short lateral margins; mandible 3-dentate, with middle tooth longest (Fig. 4).

Antenna. Geniculate, 11-segmented, without differentiated anelli, with 6 funicular segments and 3-segmented clava; radicle short, about 2× as long as broad (Fig. 2B); antennal scape ~4× as long as broad; pedicel conical, little longer than first two funicular segments combined, longer than any segment of funicle; F1 subquadrate, slightly longer than broad, F2 and F3 distinctly longer than broad, F4–F6 subquadrate, F3–F6 slightly flattened; width of flagellomeres slightly increases toward apex; F5 and F6 noticeably wider than F2–F4 (Fig. 4); all segments of funicle, at least F2–F6, and two basal segments of clava with mps; clava a little shorter than F3–F6 combined, with small oblique truncation at apical segment only (Figs 3, 4), wider than F6; flagellum and clava clothed in very short setae.

Mesosoma. Pronotum short, not conspicuously narrower than mesoscutum, almost vertical (in lateral view), with posterior edge only slightly emarginate (Fig. 3B); mesoscutum as broad as long or nearly to (in dorsal view); mesothoracic spiracle open, not concealed beneath pronotum (Fig. 1A); notauli present as depressions at extreme antero-lateral margin of mesoscutum (Figs 3A, B: arrow); meeting of axillae not visible; scutellum flat, apically pointed, with several long, vertical setae at own apex (Fig. 2B); mesopleuron enlarged posteriorly; metapleuron triangular, narrow, without visible setation (Fig. 1A); propodeum bare, with relatively large lateral parts, touching hind coxa (Fig. 1A).

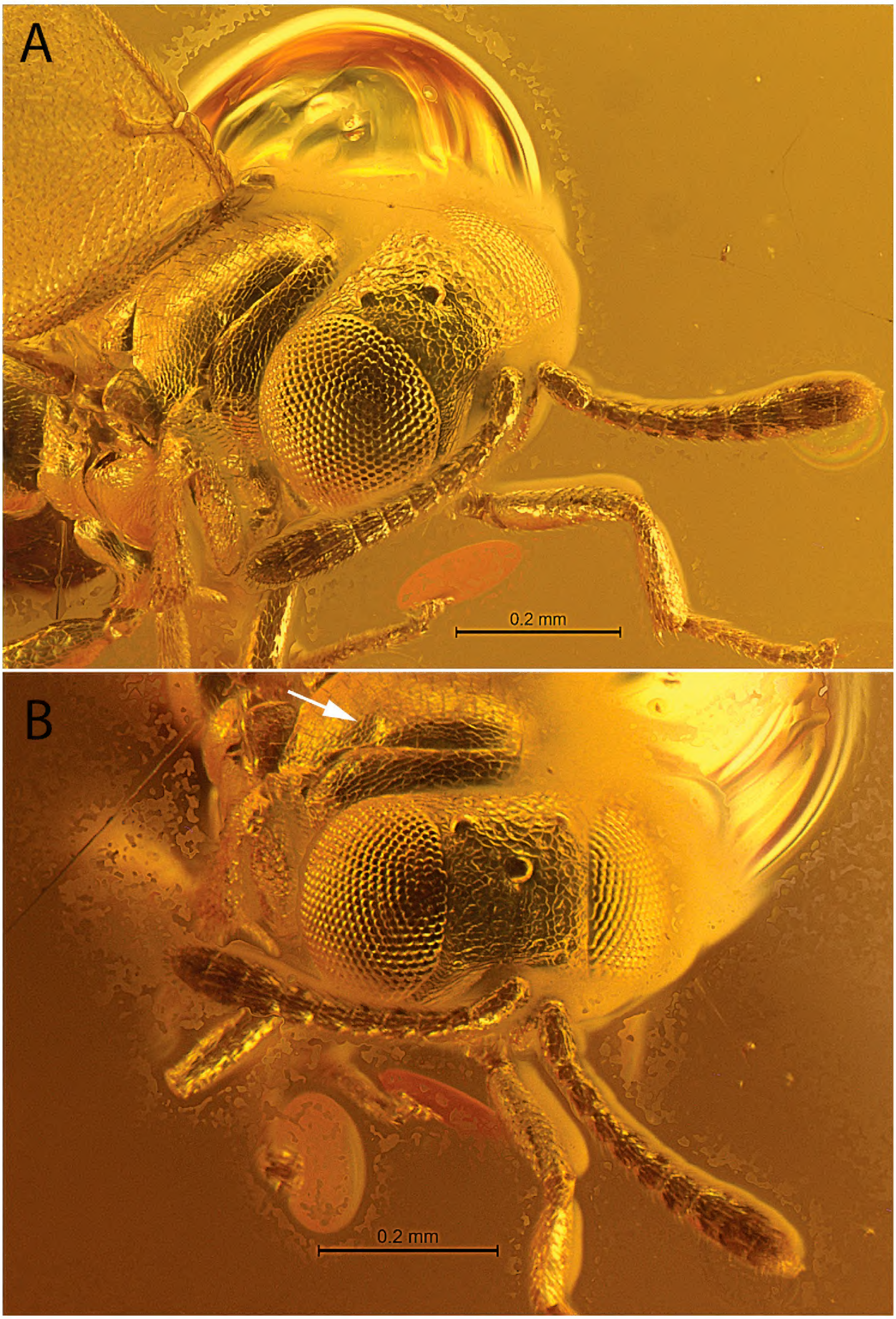

Figure 3. *Electronoyesella antiqua* gen. et sp. nov., holotype female **A** head, antennae, part of mesosoma, anterodorsolateral view **B** head, antennae, part of mesosoma, anterodorsal view (arrow indicates the notaular depression).

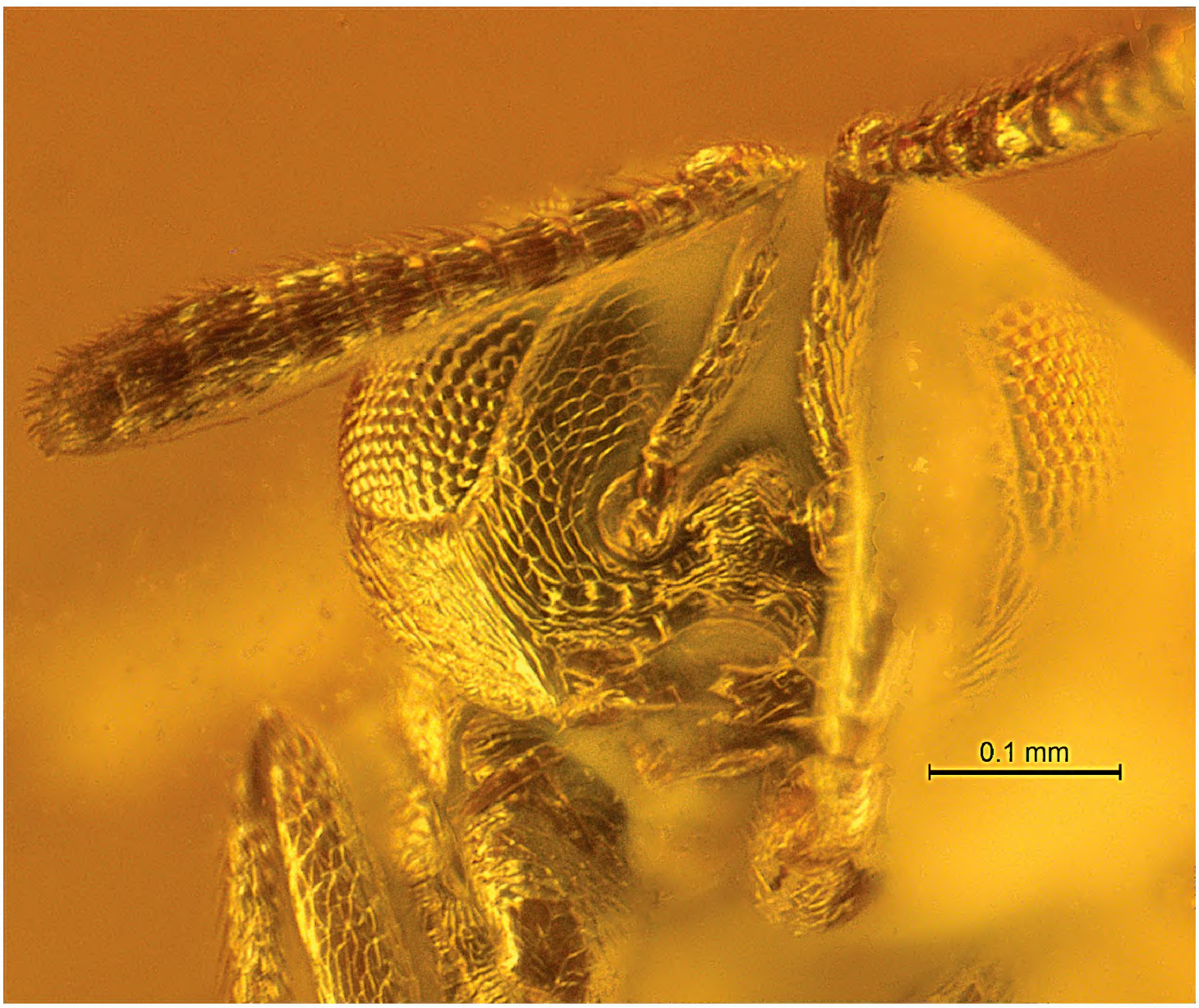

Figure 4. *Electronoyesella antiqua* gen. et sp. nov., holotype female, antennae, head anteroventral.

Wings. Fully developed, hyaline. Forewing 2.5× as long as broad; linea calva not interrupted but closed on posterior margin, without filum spinosum, with well-developed line of long setae alongside basal margin of dorsal surface (Figs 5A, B); parastigma thickened, hyaline break (unpigmented area) present; marginal vein 5× as long as broad; stigmal vein as long as marginal, with long narrow uncus consisting row of 4 uncal sensilla (Fig. 5B); postmarginal vein 1.5× as long as marginal vein, enlarged seta marking apex of postmarginal vein of forewing absent (as long as others on this vein); setae of marginal fringe short. Hindwing relatively wide; membrane of costal cell along submarginal vein with line of long setae (Fig. 5C: ls1); spur vein originating from submarginal vein visible as differentiated hyaline process, alongside this a row of 5 thickened setae (Fig. 5C: spv, ls2); apex of marginal vein with 3 hamuli; marginal fringe ~ 0.2× as long as wing width.

Legs. Mid tibial spur about as long as basal mid tarsal segment or slightly shorter, both relatively long; mesotibia with row of pegs along anteroapical edge (Figs 1B, 2A); ventral surface of mesobasitarsus and each next tarsomere with differentiated setation along anteroventral edge (Fig. 2A); apex of metatibia with one peg originating from round, deep pit and row of spine-like setae (Fig. 2A: arrows); tarsi 5-segmented.

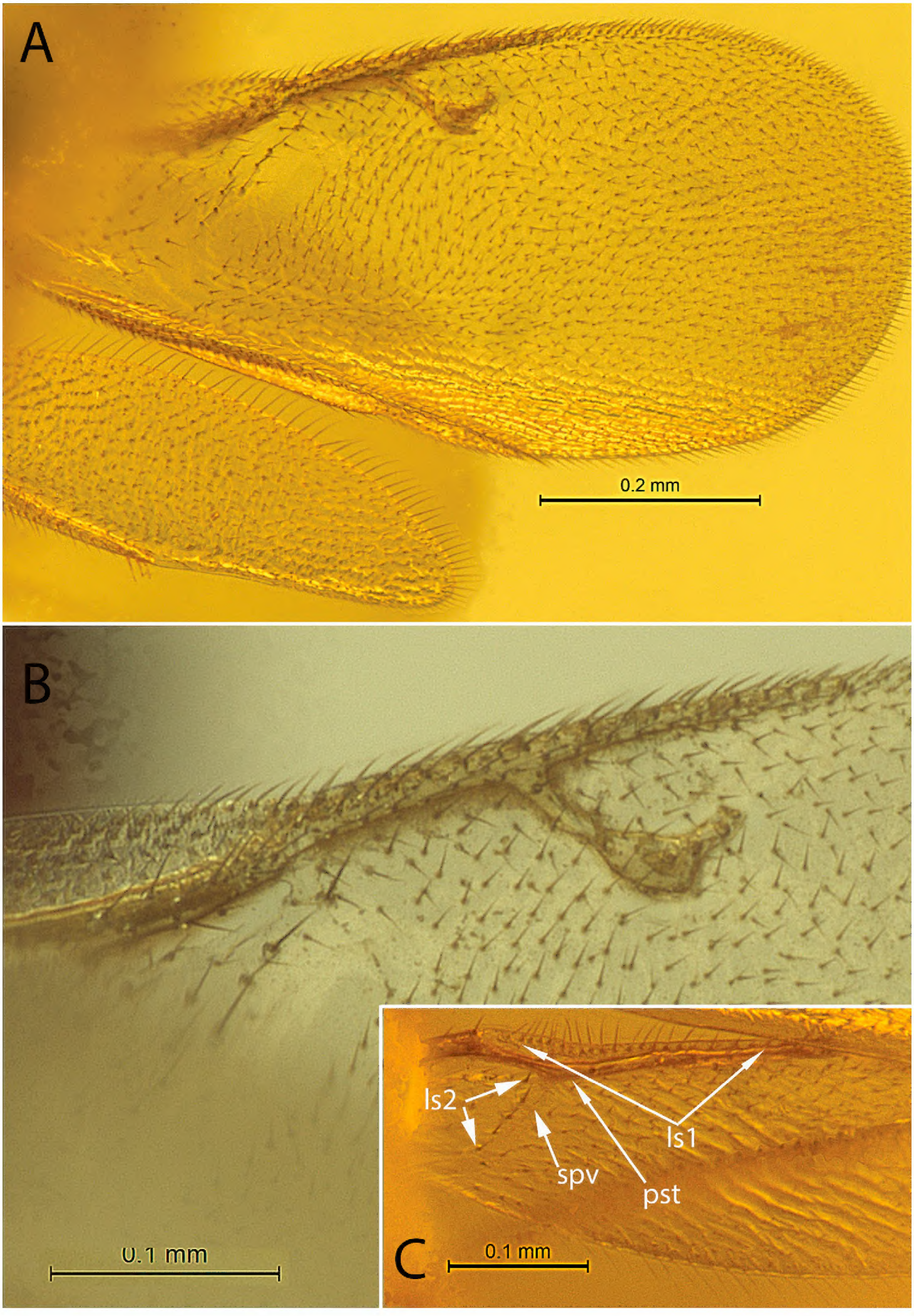

Figure 5. *Electronoyesella antiqua* gen. et sp. nov., holotype female **A** wings **B** forewing venation **C** hind wing venation (ls1, 2 – lines of setae, spv – spur vein, pst – parastigma). Scale bars: 0.2 mm (**A**); 0.1 mm (**B, C**).

Metasoma. As long as head and mesosoma together; cerci situated in apical third of metasoma, with long vertical setae (or bristles) (Figs 1A, B, 6B); syntergum (Mt8 + Mt9) v-shaped, no longer than 1/3 of metasoma; posterior margins of Mt2–Mt5 straight, parallel; Mt6 and Mt7 slightly produced, M-shaped, U-like between cerci; apex of hypopygium with developed mucro, reaching apex of syntergum (Fig. 6B); lateral margin of hypopygium bare, without row of setae; ovipositor stylet thick; ovipositor sheaths (gonostyli or third valvulae) visible in dorsal view (Fig. 6A, B: osh (v3)), as long as mesobasitarsus, connect at some angle with second valvifers (inner plates of the ovipositor, Fig. 6B: vr2), apparently, movably fused; outer plates of ovipositor not visible but (as J. S. Noyes, pers. comm. 2022, suggested) appear very slender, appear to have filamentous connection to paratergite (Fig. 6B: fc, ptrg?) running forwards to outside of cercal plate, similar to that of *Ericydnus* (Fig. 7).

Male. Unknown.

Genus composition. Type species only.

Remark. *Electronoyesella antiqua* gen. et sp. nov. from Rovno amber is the 23th non-ant hymenopteran genus (from 57, 40.4%) and 50th non-ant hymenopteran species (from 73, 68.5%), unknown from Baltic amber (Olmi 2022a, b).

Discussion. Late Eocene and extant encyrtid faunas differ (Simutnik 2021). For example, fossil Encyrtidae with reduced or shortened wings are unknown. The presence of the filum spinosum (*FS*), one of the main features of the subfamily Encyrtinae, have been found in about one third (22) of the 64 examined Eocene encyrtid specimens (males and females). In extant Encyrtidae, the number of species of Encyrtinae (with *FS*) is approximately three times more than the number of Tetracneminae species (without *FS*). The venation of the forewings and the structure of the linea calva in the fossil described here, as well as in other known Eocene Encyrtidae without *FS*, most closely resemble those of *Savzdargia* Trjapitzin, 1979; *Moraviella* Hoffer, 1954; *Monodiscodes* Hoffer, 1954; possibly some species of *Ericydnus*; and some other extant Tetracneminae. At the same time, distinct paratergites (the presence of which is one of the main features of the Tetracneminae: Trjapitzin 1968) have not been previously found in fossil females. Therefore, there is not enough morphological evidence to classify them as members of the Tetracneminae (Simutnik and Perkovsky 2018; Simutnik et al. 2022a). *Electronoyesella* has a sclerotized, ribbon-like, separated part of Mt8 along the lateral edge of the syntergum (Figs 6B, 7C: ptrg?). This structure closely resembles the paratergites of extant Tetracneminae (Fig. 7A, B: ptrg).

One of the most intriguing things in the evolution of encyrtids is what happens to the connection of tergite IX of the abdomen (Mt8) and the outer plates of the ovipositor (*OPO*) (J. S. Noyes, pers. comm. 2022). The *OPO* are completely separated from the syntergum behind the cercal plate in Encyrtinae. In Tetracneminae they are connected by the paratergite. Both features almost certainly result from advancement of cerci (Noyes 2004).

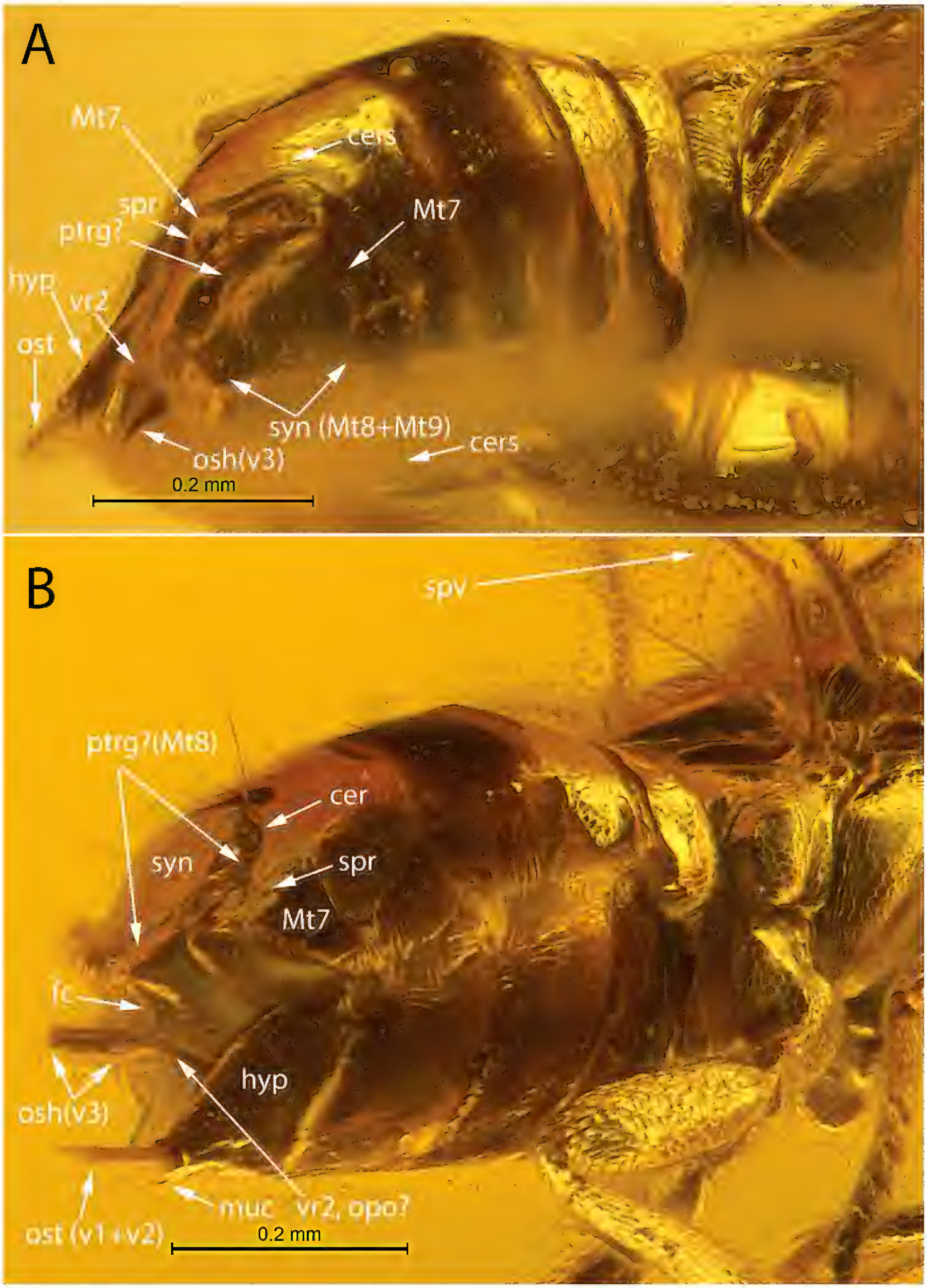

Figure 6. *Electronoyesella antiqua* gen. et sp. nov., holotype female **A** metasoma, part of mesosoma, posterodorsal (cers – cercal seta, hyp – hypopygium, osh – ovipositor sheaths, ost – ovipositor stylet, ptrg? – paratergite?, spr – spiracle, syn – syntergum, vr2 – second valvifer) **B** metasoma, part of mesosoma, posterolateral (cer – cercus, fc – filamentous connection, muc – mucro, opo? – possible, outer plate of the ovipositor, spv – hyaline spur vein; osh(v3) – ovipositor sheaths).

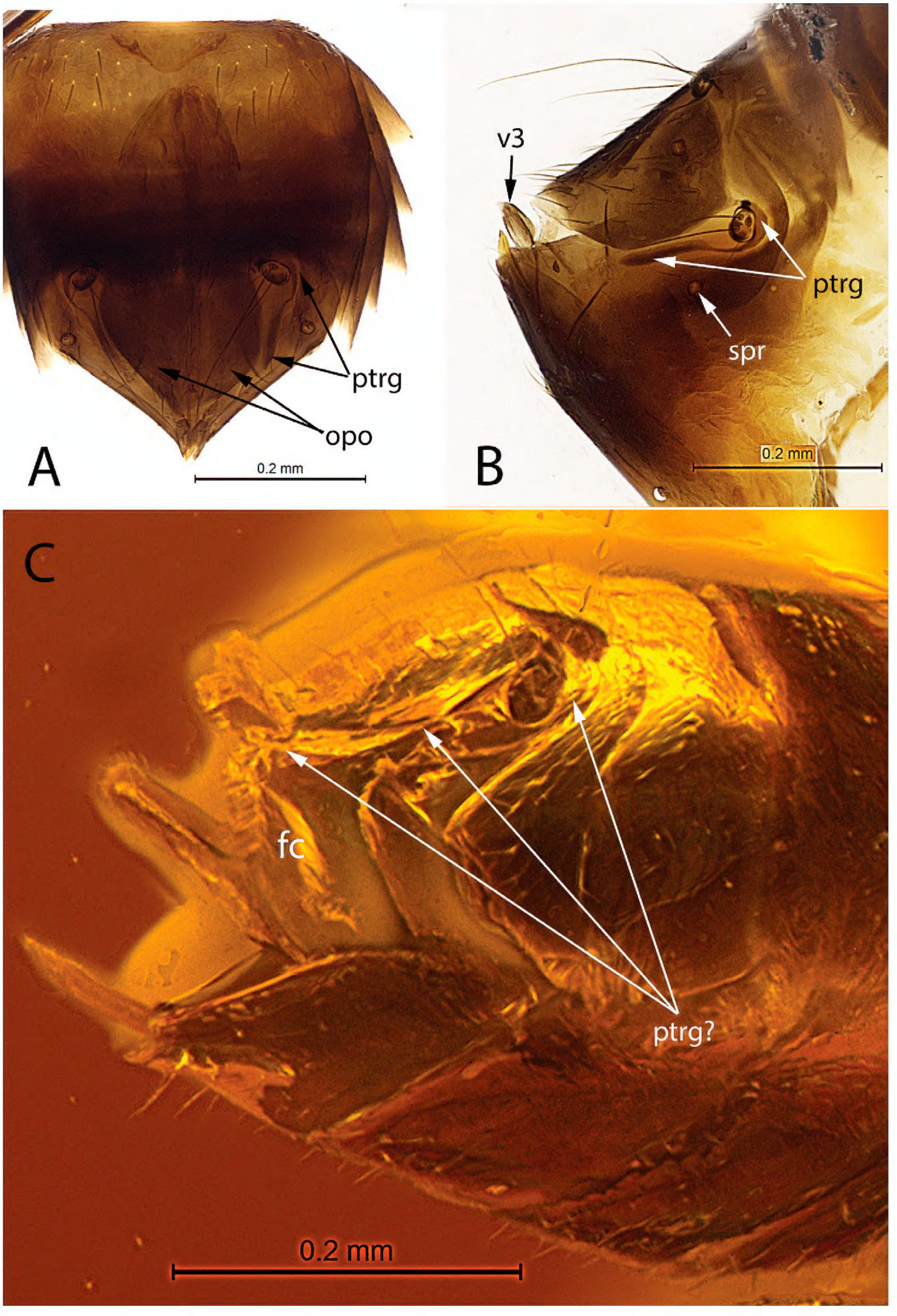

Figure 7. A, B *Ericydnus* sp., female **A** metasoma, dorsal (opo – outer plates of ovipositor, ptrg – paratergite) **B** apex of metasoma, lateral (spr – spiracle on the lateral lobe of the Mt7, v3 – ovipositor sheaths) **C** *Electronoyesella antiqua* gen. et sp. nov., holotype female, apex of metasoma, lateral (fc – filamentous connection). Scale bars: 0.2 mm.

Cerci of the earliest known middle Eocene Encyrtidae from Sakhalinian amber are close to each other, located at the very top of the gaster, similar to the ground plan state for Chalcidoidea. Then, tentatively in late Eocene, they began to shift towards the base of the gaster and the distance between them began to increase (figs 12–14 in Simutnik 2021). This process was most likely the result of adaptation to parasitization of the host, probably by Coccinea (for example, *Archaeocercoides puchkovi* Simutnik, 2022 from Rovno amber was fossilized near an undescribed crawler, see fig. 1C, D in Simutnik et al. 2022a). As the cerci advanced forward, Mt8 (or syntergum Mt8+Mt9) and then the previous terga began to separate into a dorsal part and lateral lobes (Fig. 7).

The process of cercus advancement in both Encyrtinae and Tetracneminae occurred independently and in parallel, and it began precisely in the late Eocene, since the cerci still remain in the apical or subapical position in most encyrtids from European ambers. Cerci extremely advanced to the base of the metasoma, as in many extant taxa, have not been found in known Eocene Encyrtidae.

The elongate sclerotized strip (paratergite) in Tetracneminae apparently separated from the lateral margin of the syntergum when the latter became long enough and the cercal plates advanced significantly towards the base of the gaster. The true paratergite must directly maintain a connection to tergite IX (Mt8). This connection is traceable in many species of extant *Ericydnus* around the side and anterior of the cercal plate (Fig. 7A, B) but not in any other genera where the connection, at most is at best tenuous (J. S. Noyes, pers. comm. 2022). What is possibly the paratergite of *Electronoyesella* running anteriorly to the outside of the cercal plate is very similar to the paratergite of *Ericydnus* and may provide morphological evidence for the existence of the subfamily Tetracneminae in the late Eocene.

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